

Should the biological be superseded by the phylogenetic species concept?

by D. W. Snow

A controversy of fundamental importance has been developing in animal taxonomy in recent years, and is beginning to have practical effects on ornithology. It is the argument that the long-accepted biological species concept (hereafter BSC)—as expounded notably by E. Mayr in influential publications since 1942—is fundamentally flawed and should be replaced by the concept of the 'phylogenetic species'. Hazevoet's (1995) excellent check-list of the birds of the Cape Verde Islands, the latest in the B.O.U. check-list series, adopts the phylogenetic species concept (hereafter PSC), and is the first authoritative work on an entire, though small, avifauna to do so. Cracraft's (1992) reclassification of the birds-of-paradise was the first, and still remains the only, such treatment of a bird family; Livezey (1991, 1995a, b) has applied the PSC to three tribes of the Anatidae.

The principles underlying the PSC have been expounded by Cracraft (e.g. 1983, 1987, 1992), Sluys (1991) and several other authors in the U.S.A., where the concept originated; McKittrick & Zink (1988) have advocated its use in ornithology. For most British readers the most accessible, concise introduction to it will be the clear and forceful 4-page exposition by Hazevoet in Appendix 4 to his check-list.

The purpose of the present paper is not to discuss at length the arguments for and against different species concepts. This has been done in a number of publications, including those mentioned above. Its main purpose is to mention briefly what seems a fundamental weakness of the PSC; to argue that the flaws in the BSC, while not being denied, have been exaggerated; and finally to discuss in greater detail the practical difficulties that would be encountered in any attempt to apply the PSC wholesale in avian taxonomy.

The phylogenetic species

Cracraft (1983) defines a phylogenetic species as "the smallest diagnosable cluster of individual organisms within which there is a parental pattern of ancestry and descent". Other definitions have been given, but all agree that the species should be defined as the smallest distinct group or population of common (monophyletic) ancestry; that individuals within the group must normally interbreed only with other members of their group; and that whether or not they are reproductively isolated from members of other such groups (in the sense of not interbreeding successfully with them in the event of their coming into contact) is not relevant to their species status. Species are therefore the present end-products of evolutionary change, or "evolutionary units".

It is at once obvious that, if the PSC is adopted, there will be a huge increase in the number of bird species. The species recognised will

comprise every monotypic species and many of the subspecies recognised under the biological species concept. The total will increase from *c.* 9000 to perhaps 20,000 (the latter figure based largely on guesswork; many of the 27–28,000 subspecies and monotypic species estimated by Mayr & Gerloff (1994) would not be recognised as phylogenetic species—see below). One must agree with Hazevoet (1995), however, that the sheer number of species recognised under any species concept should not in itself be a factor of any importance in the argument, which is based on principle not convenience. The critical issues are two: first, whether the PSC is biologically sounder than the BSC; and second, whether its application would be practicable.

Validity of the biological species concept

The BSC is now so well entrenched in almost all standard ornithological literature that it is taken for granted by all ornithologists who are not primarily taxonomists, and by most taxonomists too. But there are difficulties in applying it, some of which are in practice insuperable. Insuperable practical difficulties do not, of course, prove that the concept is unsound. The main criticisms of the BSC—defined as “groups of actually or potentially interbreeding natural populations which are reproductively isolated from other such groups” (Mayr 1942), with later variants which are not fundamentally different—are threefold: (1) that it is ‘process-based’, that is, based on an inferred speciation process, not on a rigorous analysis of taxonomically valid characters; (2) that the criterion of reproductive isolation is almost always untestable, so that informed guesses have to be made about the status of more or less closely related allopatric populations; and (3) that the polytypic species recognised under the BSC are not single irreducible evolutionary units; some (monotypic species) are, others (polytypic species) are not. Other objections that have been made seem less crucial, as they result largely from misapplication of the BSC through insufficient knowledge or inadequate analysis; for instance, that some polytypic species later turn out not to be monophyletic (with the likelihood that there are other such, not yet detected).

It cannot be denied that the first two of these major criticisms have some validity. The first is valid insofar as it reflects on the way in which some bird taxonomists have worked in the last 50 years; but as is argued below, cladistic analysis of taxonomic characters would in the great majority of cases almost certainly confirm the validity of the assemblages recognised by the BSC as polytypic species. The second criticism has long been recognised as the main stumbling block preventing a consistent and generally accepted application of the BSC. Decisions about the specific status of well-marked allopatric forms *are* somewhat arbitrary. They may even seem to be susceptible to changing fashions, as shown by the present trend towards giving species status to forms that have previously been treated as subspecies. In fact, such changes are usually a consequence of fuller knowledge of vocal differences and other potential isolating mechanisms; but see Collar

1997 (p. 130 in this issue). If the allopatric model of speciation is valid—and proponents of the PSC do not argue against it—this problem is to be expected. In any process of gradual change from one category to another there will be borderline cases; indeed it seems, as mentioned below, that the PSC encounters the same problem.

The third main criticism of the BSC is of a rather different kind. It concerns a matter of definition, and in my view is a main weakness of the PSC. It is not at once obvious why it is right to define species in the way the PSC defines them, rather than in the way the BSC does. Why, in fact, should all the distinct, even if only slightly distinct, 'end twigs' of the avian family tree be ranked as species? I know of no convincing answer. The idea seems to have a quasi-philosophical rather than a biological basis, and tends to be presented as dogma. Thus Cracraft (1992) writes: "The proper taxonomic framework for counting biological diversity resides with taxa of species rank, not with subspecies as required by the biological species concept." One is at liberty to disagree, and to answer that it is equally proper to use subspecies (as well, of course, as monotypic species). I suggest that this is a matter of opinion, not of science.

Defence of the BSC, at least in birds, can be argued more positively. Surely any ornithologist who has studied any group of birds with a wide geographical range (except perhaps some oceanic birds) must be convinced of the reality of what we have become accustomed to call 'polytypic species', however the units comprising them may be designated by taxonomists. The facts are so well known that it may seem unnecessary to labour them, but in the present context it is necessary. Typical Blackbirds *Turdus merula*—differing slightly in colour, but more in size and proportions; some very large, some very small, some of intermediate size; with rather different wing-shapes depending on whether they are migratory, resident, confined to oceanic islands, etc.—comprise an assemblage of forms which not only differ from other such assemblages but only make evolutionary sense on the assumption that they have been derived from an ancestral form probably centred on the west Palaearctic. This is an inference arrived at, not perhaps by cladistic analysis of all valid taxonomic characters (though such an analysis would almost certainly support the relatedness of the members of the assemblage), but by that generally very reliable computer, the unaided human brain. The fact that there are other more distinct, allopatric *merula*-like forms in the east Palaearctic and Oriental regions (*maximus* of the Himalayas, *mandarinus* of China, the *simillimus* group of the Indian subcontinent), and that it is impossible with present knowledge to know which, if any, of them might prove to be reproductively isolated, i.e. behave as separate species, from west Palaearctic *merula*, may be inconvenient for those wanting a stable taxonomy but is entirely consistent with the allopatric (Mayrian) model of speciation. The difficulty of deciding the taxonomic status of *merula*-like birds in the east is reasonably explained by their longer geographical isolation from western Blackbirds, and the very different environmental influences to which they have been subject and become adapted.

This kind of pattern of variation is all-pervasive; its details are summarised in regional handbooks, and dealt with in greater detail in monographs and other specialised publications. Attention is usually drawn to cases in which there is doubt as to the best taxonomic treatment under the BSC. Revisions are often made, as further data become available, but the main framework, based on the polytypic species, remains intact. It is reasonable to argue that the onus is on the advocates of the PSC to show, not only that the BSC is not a satisfactory framework for the classification of the different kinds of birds existing in the world today, but also that adoption of the PSC would be fraught with fewer problems.

Problems of the PSC

Cracraft's (1983) definition of a species has been quoted above. Nelson & Platnick (1981) give a very similar definition: "Species are simply the smallest detected samples [=populations, presumably] of self-perpetuating organisms which have unique sets of characters". In both definitions, the essential points are that they are the smallest groups of individuals and that their set of characters is diagnosable as unique. This seems simple enough, but the application of the definition would in very many cases be by no means easy. In the first place, the samples available are often not very large; in birds, their effective size would be further reduced by the need to compare specimens of the same age and sex class, and with plumage in a comparable state (breeding or non-breeding, degree of wear, etc.). Size differences may often be critical; but in passerines, for example, first-year birds are usually a little shorter-winged than older birds, and it is not always easy to distinguish them by plumage. Slight colour differences, which may be diagnostic in fresh plumage, may not be apparent in worn plumage. For the BSC, such sources of variation may make it hard to assess subspecies, but it is well understood that there may be differences of opinion about subspecies; it is not very important. For the PSC, where the decision affects the recognition or non-recognition of a species, the problem is acute. Two examples from the west Palaearctic may illustrate the kind of difficulty that will make application of the PSC hard to achieve with any hope of a consensus or of stability.

The kind of geographical variation shown by *Turdus merula* has already been mentioned. At the two extremes of size (based on male wing-length) are *T. m. maximus* of the Himalayas (144–167 mm) and *T. m. azorensis* from the Azores (117–127 mm). *T. m. maximus* should perhaps be treated as specifically distinct from the west Palaearctic forms under either of the debated species concepts; not only is it huge, but it differs quite markedly in plumage, and also in song and calls (Roberts 1992). But leaving aside *maximus*, *T. m. intermedius* of the central Asian mountains, which has typical *merula* plumage, is also very large, with a long bill, its wing-length (130–143 mm) falling outside the range of *azorensis*. *T. m. syriacus*, of Turkey and the Levant, may form a link with the European populations, being intermediate in size, but further study of these central and southwest Asian populations would

be needed in order to establish how isolated they are from one another and whether variation is clinal. At the bottom end of the size range, *T. m. cabreræ* of Madeira and the Canary Islands (122–129 mm) is about as small as *azorensis*; it differs from *azorensis* in having darker female plumage, a less rounded wing, and a slightly longer tail. There is some variation within the Canary Islands, which needs further study. In Europe and North Africa, between the very large eastern continental populations and the very small Atlantic island populations, there is clinal variation which the BSC recognises by a number of subspecific names. It is generally admitted that their boundaries cannot be exactly defined (e.g. Cramp 1988).

If there is some difficulty under the BSC in deciding whether the eastern Palaearctic and Oriental groups of Blackbird-like forms should be treated as conspecific with *merula*, the problem for the PSC would involve the whole range, from the Atlantic islands to China. The Azores population would certainly be a phylogenetic species; the Madeiran and Canary Islands populations would demand detailed study. They are certainly isolated from one another and further research, including molecular analysis, would very likely bring to light diagnosable differences not only between Madeira and Canary birds but perhaps also between populations of different Canary Islands. Himalayan *maximus* and Chinese *mandarinus* would certainly be given species status, while the *simillimus* group of peninsular India and Sri Lanka would probably be treated as three species, as they comprise three rather distinct allopatric groups (5 subspecies have been recognised, but at least one pair of them intergrade). Central Asian *intermedius* might well be treated as a species, as would the main bulk of the west Palaearctic mainland populations within which variation is clinal. This clinal variation would not be given formal taxonomic recognition (see below). In fact, a major re-examination of the whole complex would be necessary before any final decision could be made on the division, into a number of phylogenetic species, of what is now treated as polytypic *Turdus merula*.

The Coal Tit *Parus ater* would present a similar, perhaps even worse, problem. It has a vast continental range in Eurasia in which variation is clinal, and a number of isolated peripheral populations, some of which are very distinct. At the extreme west of the range, *P. a. hibernicus* from Ireland is diagnosable over most of that island by a yellowish wash over its plumage, but some individuals in eastern Ireland are indistinguishable from the British population, *britannicus*, and a small proportion of birds in western Britain show a slight development of the yellow colouring that is marked in Irish birds. As British and Irish birds are not all diagnosably distinct from one another they would have to be treated as conspecific. Furthermore, the Coal Tits from the Iberian peninsula are very similar to, and in fact doubtfully distinguishable from, British Coal Tits; to the east they intergrade with nominate *ater* which extends over most of Europe and Siberia. At the eastern end of the range, there is a population in northern China very distinct from nominate *ater*, with a conspicuous crest and markedly different plumage colours (*pekinensis*). It is not isolated from nominate *ater*, but

intergrades with it in Manchuria, Korea and the Amur region. Under the PSC all these populations, from Ireland and Iberia east to China, would have to be treated as conspecific, and no formal recognition would be given to their many and striking differences.

Attention would then have to be given to the isolated southern populations. They comprise what are usually recognised as 14 subspecies, ranging from northwest Africa east through central Asia to southern China and Taiwan. Some are well isolated and distinct, and would certainly be treated as phylogenetic species, e.g. *cypristes* from Cyprus and *ptilosus* from Taiwan. Others would be problematical. For instance, the two northwest African forms, *atlas* and *ledouci*, are very distinct from all others. They differ conspicuously, but superficially, from each other, *ledouci* from mesic woodlands in Tunisia and eastern Algeria having a bright yellow wash over its plumage that is totally lacking from the very grey-plumaged, and also slightly larger, *atlas* from the Moroccan Atlas Mountains, which lives mainly in drier woodlands and at higher altitudes than *ledouci*. These two forms have stouter bills than their European relatives and differ from them in voice (Cramp & Perrins 1993). Under the PSC they would probably, at least until a short time ago, be treated as two species. There are, however, complications. It has recently been found that some populations apparently isolated in patches of rather dry montane woodland in Algeria, between *atlas* and *ledouci*, are intermediate in plumage but closer to *atlas* in size. They may constitute a third distinct form (Cramp & Perrins 1993), but have not been well studied. The Coal Tits from the Crimea, where they are well isolated from other populations, are usually considered to represent a distinct subspecies, but it is not well-marked. Further east, from the Caucasus down into the mountains of Iran, there is a trend towards brown-backed and thick-billed populations, apparently adapted to dry oak woodlands. Some at least of them are probably well isolated from others by intervening desert or semi-desert; but they have not been studied in detail and the three subspecies recognised may well need revision.

It is clear that very considerable research would be needed by anyone undertaking to reclassify the Coal Tits according to PSC principles. One can only guess at how many species would result; probably at least 15, and the number might well be altered by later research.

These examples were chosen because I happened to be familiar with them, and they may for that reason be suspected of being biased so as to exaggerate the problems of using the PSC. To check on this, I made an analysis of the 94 European breeding species in the two volumes (5 and 7) of *Birds of the Western Palearctic* containing the Blackbird and Coal Tit, using the detailed information given in the sections on geographical variation, nearly all by C. S. Roselaar. I tried to see how many phylogenetic species they would constitute and how many problems, and of what kind, would be encountered in attempting such a classification. To anticipate what is dealt with in a little more detail below, it must be noted again that the PSC gives no taxonomic recognition to geographical variation within continuous populations, however well marked it may be; all distinct and isolated populations

are, as we have seen, given species status. The analysis gave the following results, summarised here in broad categories because hardly any two cases are exactly alike.

No. of spp. (BSC)	Nature of geographical variation	Presumed PSC treatment
21	None or very slight (monotypic species)	Same number recognised
18	Slight; mainly or entirely clinal	Ditto; slight geog. variation ignored
4	Moderate; mainly or entirely clinal	Ditto; moderate geog. variation ignored
5	Marked; mainly or entirely clinal (e.g. <i>Parus montanus</i>)	Ditto; marked geog. variation ignored
13	Slight, mainly clinal, but with more distinct disjunct populations (e.g. <i>Motacilla cinerea</i> , <i>Erithacus rubecula</i>)	Disjunct populations recognised as species; each BSC sp. probably becoming 2-4 PSC spp. (further study needed)
8	Moderate or marked, with some disjunct populations (e.g. <i>Monticola solitarius</i> , <i>Turdus merula</i> , <i>Parus ater</i>)	Disjunct populations recognised as species; each BSC sp. probably becoming 2-c. 15 PSC spp. (further study needed)
12	Marked; in distinct subspecies groups, some clinal variation within groups or areas of secondary contact/intergradation (e.g. <i>Cercotrichas galactotes</i> , <i>Saxicola torquata</i> , <i>Parus caeruleus</i> , <i>Lanius excubitor</i>)	Impossible to predict, would need detailed study
13	Complex and (except in 2 cases) marked; mainly continental ranges, probably with complex evolutionary histories (e.g. <i>Galerida cristata</i> , <i>Motacilla flava</i> , <i>Sitta europaea</i> , <i>Remiz pendulinus</i>)	Ditto

The above figures indicate that about half of the species recognised under the BSC would need further study before any attempt could be made at a PSC classification; many would have to be the subject of major revisions. Such research would certainly lead to improved understanding of the assemblages of forms involved; it seems unlikely that it would lead to stability in species-level nomenclature in the coming decades.

In making this analysis, the strong impression was gained that the great majority of polytypic species recognised under the BSC, although not based on cladistic analysis, would stand up to such an analysis and be shown to be monophyletic. In a few cases, there is doubt about whether the species recognised should be split, or merged with another species, but not about their monophyly. Before the polytypic species is rejected by proponents of the PSC, I suggest that it would be desirable to subject a representative selection of widespread polytypic species (as

recognised under the BSC) to cladistic analysis, rather than reject the concept wholesale because of detected errors and questionable methods previously used in avian taxonomy.

Recognition of subspecies under the PSC

It has been widely recognised that the subspecies is not an altogether satisfactory taxonomic category, mainly because (1) geographical ranges of subspecies cannot be clearly delimited in clinally varying populations; (2) there is no general agreement (though some suggestions have been made) on what degree of difference between populations should be accepted as justifying their subspecific separation; (3) it is very often impossible to decide whether or not isolated and well-marked subspecies should be given specific rank. Means have been suggested for dealing with these problems—e.g. Huxley's (1938) notation for clines; the use of special terms such as semi-species or megasubspecies for very distinct forms thought to be verging towards specific status—but they have not been generally adopted. Lack (1968) and later authors have concluded that the objections are so serious that the subspecific terminology at present in use has outlived its usefulness and should be replaced by some more appropriate method of categorising variation below the species level.

Under the PSC, the subspecies at present has a shadowy existence in a kind of limbo. In his general, theoretical discussion of the phylogenetic species, Cracraft (1987) mentions subspecies only in a footnote, which is devoted mainly to the problems discussed above and implies that the naming of subspecies would have no place in the PSC. In his re-classification of the birds-of-paradise (1992), he is more explicit, but still with some ambivalence: "Adoption of the phylogenetic species concept solves a long-standing source of contention within systematics, namely the taxonomic status of subspecies. Because phylogenetic species are basal (smallest recognizable) differentiated taxonomic units, subspecies could only be applied as arbitrary descriptors of within-species variation. Within that context, therefore, they serve little useful purpose." In his Cape Verde Islands check-list Hazevoet (1995), after summarising the subspecies problem, concludes that "trinomials can perhaps still serve a minor role within a continuum showing clinal or otherwise geographical variation", but whenever he uses it he places the word subspecies in inverted commas, implying non-recognition of it as a valid taxonomy category.

Both authors therefore recognise the existence of geographical variation within the phylogenetic species, but decide that it does not need formal taxonomic recognition. Under the BSC, some kind of formal recognition of within-species variation is clearly essential, and the subspecies, for all its shortcomings, is the only method that has found widespread, though not uncritical, acceptance. If the PSC were brought into general use there would surely be a need, in formal listings of bird species, to draw attention in some way to clinal variation, in which differences between ends of a cline may be as marked as, or in some cases considerably greater than, differences between taxa that

would rank as species. Would it be sensible, for example, to give no formal recognition to the striking difference between the small, dark, brownish Willow Tits *Parus montanus* of lowland western Europe and the large, very pale, greyish populations of eastern Siberia, because they are connected by a range of intermediate forms?

Use of the PSC in check-lists

Systematic listing of the avifauna of the Cape Verde Islands (Hazevoet 1995), with comparatively few breeding species, is not very much affected by the choice of species concept. Hazevoet recognises 14 "diagnosably distinct endemic taxa", which he treats as phylogenetic species. Four of them (*Apus alexandri*, *Alauda razae*, *Acrocephalus brevipennis*, *Passer iagoensis*) are distinct enough to be treated as endemic species in *Birds of the Western Palearctic*, the latest standard work covering the Cape Verdes. Three of the remaining 10 are oceanic birds (*Pterodroma*, *Calonectris*, *Puffinus* spp.), which present their own problems of classification; see, for example, Shirihai *et al.* (1995) on the *Puffinus assimilis/lherminieri* complex. The remaining 7 land-birds include such forms as *Buteo (b.) bannermani*, *Tyto (a.) detorta* and *Falco (p.) madens*, which under the BSC are currently treated as well-marked subspecies.

Hazevoet lists 8 "taxa of which the Cape Verde population has been treated as a 'subspecies', which is, however, not diagnostically distinct". Some of these are certainly very poor subspecies; he synonymises them with their respective continental species. But among them is the Grey-headed Kingfisher *Halcyon leucocephala*, which differs to a certain extent in coloration and measurements (especially bill-length in which there is little overlap) from its Afrotropical relatives. It is resident, having lost the migratory habit of the mainland populations. Using traditional methods of diagnosis based on measurements and plumage, and confining comparisons to adult specimens in fresh plumage, it seems quite likely that it would prove to be diagnosably distinct. Molecular analysis might be expected to support the distinction. In passing it may be suggested that it was by good fortune that the other 7 Cape Verde land-bird subspecies all proved to be poor ones; applying the PSC to some other island avifaunas might have been trickier.

A case like this suggests that proponents of the PSC, when listing local avifaunas, will be confronted with problems similar to those that face the conventional BSC taxonomist; but for the former the judgment is about the existence or otherwise of a species, and a mistake is more serious.

Application of the PSC to an inadequately known family

Cracraft's (1988) re-classification of the birds-of-paradise highlights some of the difficulties of applying the PSC to a family in which ranges and geographical variation are incompletely known. His analysis results in the recognition of 90 species, double the number recognised under

the BSC (40, Mayr 1962; 42, Gilliard 1969; 45, Sibley & Monroe 1990). The increase in number of species comes mainly from the elevation to species rank of a large number of BSC subspecies.

Such a procedure is unjustified in the present state of knowledge. The collection and taxonomic study of birds in New Guinea to date involves a tiny fraction of the area of the island. In many cases nothing is known of the possible presence, or variation, of populations between the places where forms usually treated as subspecies have been collected. There may well be continuous populations, with intergradation; in such cases two or more phylogenetic species would have to be merged. Conversely, as Cracraft notes, further collecting may reveal new forms, which would be given species status under the PSC if their allopatric status vis-à-vis closely related forms could not on available evidence be disproved. In all such cases the mistakes that may result from inadequate knowledge are more serious for the PSC than for the BSC. For instance, Cracraft recognises three species of *Paradigalla*. A recent thorough analysis of this little known genus (Frith & Frith 1997) has shown that one of the three, a controversial BSC subspecies based on few specimens, is in fact indistinguishable from one of the two other (clearly diagnosably distinct) forms. The three PSC species should be reduced to two; under the BSC, the only change necessary is to reject one doubtful subspecies.

Cracraft's treatment seems in some cases inconsistent with PSC principles, probably because subjective judgment still seems necessary in spite of professions of rigorous analysis. Thus the two populations of *Lycorax pyrrhopterus*, on Batjan and Halmahera, seem from his account to be diagnosably distinct; but he does not treat them as two phylogenetic species. The reason ("These two populations are united here until further information is available as to the extent of their behavioural and genetic differentiation") surely applies equally to forms that he does treat as separate phylogenetic species.

One result of elevating to species rank very similar subspecies of one species within a genus, such as the four forms of *Paradisaea minor*, is that the resulting genus consists of some very distinct and some all-but-identical species. There is then an obvious need to recognise a category intermediate between the phylogenetic species and the genus, as Cracraft does by placing the four above-mentioned forms in a 'species group'. This is likely to be a common problem for the PSC. If species groups of this sort are formally recognised, the arrangement that will result is likely to parallel, and in many cases become identical with, the BSC arrangement of polytypic species and their component subspecies; the PSC would simply have elevated each category to a higher rank. And all this would be due to what seems to me to be a dogma rather than a reasoned decision, that species *must* be the smallest diagnosable clusters or end-products of the evolutionary tree.

Conclusion

The arguments set out above lead, I suggest, to the conclusion that the biological species concept, while not perfect, is still useful and

meaningful; and that adoption of the phylogenetic species concept is likely to be beset by problems that are equally or more intractable; at the very least, they will require years of research in order to establish which taxa, now treated as subspecies, have uniquely diagnosable characters. Even if this could be done, there would be the risk that future research and analysis, using more sophisticated methods, might necessitate constant changes. Examples of this are in fact already apparent in recent publications. Thus, in their analysis of genetic and phenotypic differences between related bird populations on either side of the Bering Strait, Zink *et al.* (1995) find that, on the basis of their DNA, the populations of *Anthus rubescens* would be considered different phylogenetic species, but no morphological differences are detectable. For some reason they do not do so on the basis of DNA alone (perhaps sensing that this would open the floodgates?), but write: "If morphological or other genetic differences between these populations are found, we think that they should be treated as separate species". How many other such cases are there which may come to light; and how many that will not come to light? From a purely practical point of view, the adoption of the PSC would mark the end of the relative taxonomic stability that has been achieved by the acceptance of the biological species concept. From a theoretical point of view, its adoption would not, in my opinion, signal any advance in our understanding of evolutionary processes at the species level.

Summary

The biological species concept (BSC), which has been generally accepted as the basis of avian taxonomy for over 50 years, has recently been challenged as being fundamentally flawed, and the proposal has been made that it should be replaced by the phylogenetic species concept (PSC). Under the PSC, polytypic species are not recognised, the species being defined as the smallest diagnosably distinct cluster or population of individuals that normally interbreed only among themselves. Reclassification of birds on PSC principles would at least double the number of species, but this is not a reason to reject it.

It is argued here that the concept of the polytypic species is based on recognition of a real and widespread phenomenon, and is not invalidated by the old-fashioned and inadequate methods that have often been used in its study. The problems encountered are just those that would be expected. It is also argued that the definition of what constitutes a species under the PSC is arbitrary and includes an element of dogma, and has no more inherent validity than definitions based on the BSC.

Wholesale application of the PSC to birds would meet with serious problems. There are many polytypic species (as recognised by the BSC) in which much further, and difficult, research would be needed if they were to be reclassified according to PSC principles, decisions about what is or is not a diagnosably distinct population being impossible on present knowledge. Even if this were done, there would always be the likelihood that further research would entail further changes. All such changes under the PSC would involve changes in the number of species recognised, and so are more serious than changes under the BSC, which would usually affect the recognition of subspecies, a category well known to be subject to change. The relative stability in species-level taxonomy achieved under the BSC would be lost, certainly for decades. To judge from publications to date in which the PSC is adopted, there would still be a need for the sort of subjective judgments that have been condemned as a fundamental weakness of the BSC. It is concluded that there is at present no case for replacing the BSC by the PSC.

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References:

- Collar, N. J. 1997. Taxonomy and conservation: chicken and egg. *Bull. Brit. Orn. Cl.* 117: 122-136.
- Cracraft, J. 1983. Species concepts and speciation analysis. *Current Ornithology* 1: 159-187.
- Cracraft, J. 1987. Species concepts and the ontogeny of evolution. *Biology and Philosophy* 2: 329-346.
- Cracraft, J. 1992. The species of the birds-of-paradise (Paradisaeidae): applying the phylogenetic species concept to a complex pattern of diversification. *Cladistics* 8: 1-43.
- Cramp, S. 1988. *The Birds of the Western Palearctic*. Vol. 5. Oxford Univ. Press.
- Cramp, S. & Perrins, C. M. 1993. *The Birds of the Western Palearctic*. Vol. 7. Oxford Univ. Press.
- Frith, C. B. & Frith, D. W. 1997. The taxonomic status of the bird of paradise *Paradigalla carunculata intermedia* (Paradisaeidae) with notes on the other *Paradigalla* taxa. *Bull. Brit. Orn. Cl.* 117: 38-48.
- Gilliard, E. T. 1969. *Birds of Paradise and Bowerbirds*. Weidenfeld & Nicolson, London.
- Hazevoet, C. J. 1995. The birds of the Cape Verde Islands. BOU Check-list no. 13.
- Huxley, J. S. 1938. Clines: an auxiliary taxonomic principle. *Nature* 142: 219.
- Lack, D. 1946. The taxonomy of the Robin *Erithacus rubecula* (Linn). *Bull. Brit. Orn. Cl.* 66: 55-65.
- Livezey, B. C. 1991. A phylogenetic analysis and classification of recent dabbling ducks (Tribe Anatini) based on comparative morphology. *Auk* 108: 471-507.
- Livezey, B. C. 1995a. Phylogeny and evolutionary ecology of modern seaducks (Anatidae: Mergini). *Condor* 97: 233-255.
- Livezey, B. C. 1995b. Phylogeny and comparative ecology of stiff-tailed ducks (Anatidae: Oxyurini). *Wilson Bull.* 107: 214-234.
- Mayr, E. 1942. *Systematics and the Origin of Species*. Columbia Univ. Press.
- Mayr, E. 1962. Family Paradisaeidae, in E. Mayr & J. C. Greenway, Jr. (eds), *Check-list of Birds of the World*. Vol. 15. Museum of Comparative Zoology, Harvard.
- Mayr, E. & Gerloff, J. 1994. The number of subspecies of birds. *Bull. Brit. Orn. Cl.* 114: 244-248.
- McKittrick, M. C. & Zink, R. M. 1988. Species concepts in ornithology. *Condor* 90: 1-14.
- Nelson, G. J. & Platnick, N. I. 1981. *Systematics and Biogeography: Cladistics and Vicariance*. Columbia Univ. Press.
- Shirihai, H., Sinclair, I. & Colston, P. R. 1995. A new species of *Puffinus* shearwater from the western Indian Ocean. *Bull. Brit. Orn. Cl.* 115: 75-87.
- Sibley, C. G. & Monroe, B. L., Jr. 1990. *Distribution and Taxonomy of Birds of the World*. Yale Univ. Press.
- Sluys, R. 1991. Species concepts, process analysis, and the hierarchy of nature. *Experientia* 47: 1162-1170.
- Zink, R. M., Rohwer, S., Andreev, A. V. & Dittmann, D. L. 1995. Trans-Beringia comparisons of mitochondrial DNA differentiation in birds. *Condor* 97: 639-649.

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